

## AN ANNOTATED CHECKLIST OF THE FOSSIL TORTOISES OF CHINA AND MONGOLIA

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*Abstract.*—A review of published descriptions in some unavailable or obscure journals was done to collate and summarize useful morphological data on the fossil tortoises of Mongolia and China. Four genera of testudinids are recognized and tentatively diagnosed: *Testudo*, *Geochelone*, *Indotestudo*, and 'Manouria.' *Sinohadrianus* and *Kansuchelys* are considered synonyms of 'Manouria,' which is diagnosable, but not defined by shared derived characters.

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Fossil land tortoises (Testudinidae) appear suddenly in Early Eocene sediments of North America and China. By the Late Eocene tortoises are also known from Europe (de Broin 1977; Mlynarski 1955; Schleich 1981) and North Africa (Andrews 1906), while persisting in North America and China. Fossil tortoises are among the most commonly encountered Tertiary remains and may be employed as useful stratigraphic markers (Hutchison 1980).

Although much is known of the structure, distribution, and evolutionary relationships of European and North American tortoises (Auffenberg 1963, 1966, 1971, 1974, 1976; Bramble 1971, in press; Van Devender *et al.* 1976), comparatively little is known of their Chinese counterparts. The acquisition of detailed information on the 24 named Chinese taxa has been hampered by two factors. Firstly, is the difficulty in examining the material. During the past forty or so years there has been very little interchange between oriental and occidental paleobiologists. Travel to the Institute of Vertebrate Paleontology and Paleoanthropology in China, where 17 of the 24 types reside, has not been possible until recently. Thus, western students of tortoise evolution, familiar with North American and European fossil remains have not had the opportunity to examine Chinese material. Secondly, the original descriptions of Chinese fossil land tortoises have often been published in journals not readily available to western researchers. The purpose of this checklist is to summarize the information published in those journals, to facilitate a useful synthesis.

The following list is arranged alphabetically by species name. Comments on materials, other than American Museum of Natural History specimens, are based on published figures and diagnoses. For this reason and because some of the figures are poor, remarks concerning morphology are often incomplete. The present status of the species and prevailing theories of relationship, if any, are noted. Generic names in quotes indicate that I have been unable to corroborate monophyly of the genus. The obvious limitations inherent in a checklist like this require that the reader regard generic assignments as tentative. Specimens in the American Museum of Natural History, New York (AMNH) were examined. Other unexamined material is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP), Zaklad Paleobiologii, Polska Akademia Nauk, Warszawa (Z. Pal.), and the Geological Survey of China. The bone and scute

terminology of Zangerl (1969) and the *Catalogue of American Amphibians and Reptiles* is followed.

*Kansuchelys chiayukuanensis* Yeh, 1963a:28

*Type*.—IVPP V.1006, right posterior carapace and plastron, damaged. Two paratypes are designated (IVPP 1006a, IVPP 1006b). *Type locality*: Shih-erh-mach'eng, North of Hui-hui-p'u, Chia-yu-kuan, Kansu. *Horizon*: Unknown (? Oligocene or Late Eocene).

*Remarks*.—A very primitive tortoise, judging from the entirely hexagonal neurals, which are short-sided anteriorly, and the primitive suprapygal pattern (two suprapygal elements with the larger dorsal element embracing the ventral elliptical element. Extended discussion of this and other features will be the subject of another paper). Numerous other features show resemblances to '*Manouria*' (*sensu* Auffenberg 1971) species. These include the anal scute which is about the same median length as the femoral scute and the pleural scutes which are contacted by only the fifth and sixth marginals. The gular scutes but not the pectoral scutes overlap the entoplastron. The cervical scute is very large but slightly longer than broad.

*Testudo chienfutungensis* Yeh, 1963a:44

*Type*.—IVPP V.1030, carapace with connected plastron, damage to anterior carapace, posterior peripherals missing. *Type locality*: Taben-buluk, Tunhuang, Kansu. *Horizon*: Miocene (?).

*Remarks*.—Yeh (1963a) allocated this species to the genus *Testudo* on the basis of the position of the pleuro-marginal sulcus. Both Yeh (1963a) and Bohlin (1953) felt that the elongate shell, the presence of intergular scutes and the hexagonal neurals were abnormal conditions. Irrespective of the presence or absence of intergular scutes, the gular scutes overlap the entoplastron. Auffenberg (1974) thought this species may not be a testudinid. Bohlin (1953) noted two suprapygals arranged serially and of about equal size, whereas Yeh (1963a) characterized the suprapygal as entire. The four-sided fourth neural is odd for a tortoise, in which this neural is usually eight or six-sided. This species does possess some tortoise-like features, but most are shared primitive features. For example, the anal scute is much broader than the femoral scute and there is very little constriction at the anal and gular scutes posterolateral borders. Auffenberg's (1974) reservations concerning this species are understandable.

*Testudo demissa* Gilmore, 1931:239

*Type*.—AMNH 6670, right xiphiplastron (probably of large male). *Type locality*: Ardyn Obo, Chinese Postroad, Outer Mongolia. *Horizon*: Ardyn Obo formation, Lower Oligocene.

*Remarks*.—This species is distinguished on the basis of a thickened and downturned anal region of the plastron and very short anal scutes. Both these characters appear in many unrelated tortoises and are even more prominent in large males of these unrelated species. Mlynarski (1968) synonymized *T. demissa* with *Geochelone insolitus* (Matthew and Granger, 1923), and allocated both species

to the genus *Geochelone*. Auffenberg (1974) tentatively allocated *G. insolitus* and *T. demissa* to the subgenus *Manouria*. The extreme narrowness of the anal scutes contradicts Auffenberg's allocation.

*Testudo hipparionum* Wiman, 1930:41

*Type*.—IVPP (Catalogue number not published), complete shell. Type locality: Shansi, Wu-Hsiang-Hsien, E 2 li (1 li equals about one-third of a mile) Huo-Shen-Miao-Kou. Horizon: Pliocene.

*Remarks*.—Very poorly described by Wiman (1930) but re-described and figured from non-type material by Yeh (1963a). Yeh (1963a) also refers four IVPP specimens to this species (IVPP V.1017, V.1018, V.1020, and V.1024). IVPP V.1024 includes a skull and parts of the appendicular skeleton. Yeh (1963a) noted that this may be the most common tortoise in northern Chinese red clay beds. Gilmore (1934) and Auffenberg (1974) contended that other tortoises named by Wiman may be variants of *T. hipparionum*. The shape and size of the cervical and questionably interpreted pleuro-marginal scute contacts support the allocation of this species to the genus *Testudo* (sensu stricto). Other characters include two suprapygial elements, the larger embracing the smaller elliptical element (primitive); the gular scutes, but not the pectoral scutes, overlap the entoplastron; some plastral constriction at the anal and epiplastral border; three marginals (numbers 5, 6, and 7) contact the second pleural scute (primitive); and neural formula 4-8-4-8-4-8-?4-?6.

*Testudo honanensis* Wiman, 1930:43

*Type*.—IVPP (Catalogue number not published), partial carapace and nearly complete plastron. Type locality: locality 12, Honan, Hsin-An-Hsien, Shan-Yin Kou. Horizon: Unknown (? Miocene).

*Remarks*.—Yeh (1963a) referred three IVPP specimens (IVPP V.1025, V.1026, V.1027) to this species but Auffenberg (1974) contended that Yeh's usage of this name is synonymous with *T. sphaerica*. Mlynarski (1955) believed that this form is assignable to the *antiqua-graeca* phyletic line. Cervical shape and size, and an anal scute having a greater median length than the femoral scute support the allocation of this species to the genus *Testudo*. The hexagonal third neural is unusual. The neural formula is 4-8-6-8-?4-6-6-6.

*Testudo hypercostata* Wiman, 1930:35

*Type*.—IVPP (Catalogue number not published), nearly complete shell. Type locality: locality 114 south, Shansi, Ho-Ch'u-Hsien, SE 60 li (1 li equals about one-third of a mile) of Nan-Skha-Wa, 1 li from Ma-Hua-T'an. Horizon: Pliocene.

*Remarks*.—Yeh (1963a) contended that this species is specialized because it possesses a supernumerary neural. Auffenberg (1974) disagreed and claimed that this form is conspecific with *T. shensiensis*. The neural formula is 4-8-4-8-4-6-6-6-4. The anal midline length is only slightly less than the femoral length. The entoplastron is not overlapped by either the gular or pectoral scutes. There is some constriction at the lateral borders of the epiplastral and anal regions. The second pleural scute is contacted by three marginal scutes.

*Testudo insolita* Matthew and Granger, 1923:5

*Type*.—AMNH 6275, parts of carapaces and plastra of several individuals. Type locality: Promontory Bluff, on the Sair-Ussu-Kalgan trail, about 150 miles from Sair-Ussu and 350 miles from Kalgan, Ardyn Obo basin, Mongolia. Horizon: Oligocene.

*Remarks*.—Gilmore (1931) felt the poor description of this species made the determination of its affinities impossible. Mlynarski (1968), nonetheless, synonymized *Geochelone demissa* (Gilmore, 1931) with *T. insolitus*. The entoplastron is not overlapped by the pectoral scutes, which narrow abruptly as they extend medially. The xiphi-hypoplastral sutures are located far posterior from the femoral-abdominal sulcus. The cervical scute is long and thin and recessed from the anterior margin of the carapace. Mlynarski's (1968) assertion that the neural bones are octagonal, hexagonal and tetragonal cannot be confirmed until fossil material of that region of the shell is found. This large tortoise with abbreviated anal scutes is referable to *Geochelone*, as Auffenberg (1974) and Mlynarski (1968) suggest.

Chkikvadze (1972) described *Ergilemys*, type-species *G. insolitus*, and considered that Early Oligocene genus ancestral to *Prototestudo* Chkikvadze (1970), '*Manouria*,' *Geochelone*, and *Indotestudo*. The distinctive features of *Ergilemys* are primitive characteristics. Mlynarski (1976) demotes *Ergilemys* to a subgenus of *Geochelone*. In addition to the five species assigned to *Ergilemys* by Chkikvadze, de Broin (1977) has included another newly named species. Thus, although its affinities are often considered, *T. insolita* remains enigmatic.

*Testudo kalganensis* Gilmore, 1931:247

*Type*.—AMNH 6701, anterior part of carapace, most of anterior lobe of plastron minus entoplastron, and carapacial and plastral parts of right side of bridge. Type locality: Kalgan Area, North China. Horizon: Tertiary (?).

*Remarks*.—Gilmore (1931) did not remark upon the relationships of this species; such reticence is understandable given the greatly thickened and extraordinarily sculptured shell. Auffenberg (1974), citing two of his earlier works (1962 and 1963), assigned this species to the *turgida* phyletic line of the subgenus *Hesperotestudo*. The pectoral scute overlaps the entoplastron, a feature that characterizes *Indotestudo* and *Testudo horsfieldii*. The gular scutes also overlap the entoplastron. The cervical is long and thin and slightly recessed. Although questionable, it is possible that the femoral scutes do not contact the inguinal scutes, a feature common to *Testudo*. Assignment to *Hesperotestudo* seems premature.

*Testudo kaiseni* Gilmore, 1931:236

*Type*.—AMNH 6352, nearly complete carapace and plastron. Type locality: Ardyn Obo basin, Chinese Postroad, Outer Mongolia. Horizon: Ardyn Obo formation, Lower Oligocene.

*Remarks*.—Auffenberg (1974) questionably referred this species to *Indotestudo*, probably because the pectoral scute overlapped the entoplastron. Earlier, Glaessner (1935) contended that *T. kaiseni* was a member of the *Testudo antiqua*

group, contrary to Mlynarski (1955). The femoro-abdominal sulcus, which is faintly visible on the type, was not figured by Gilmore (1931, fig. 17, p. 238). The anal scute is about the same median length as the femoral scute, perhaps slightly greater. Neither the gulars nor the pectorals overlap the entoplastron. The neural formula is 4-7-4-7-5-6-?-?. In most tortoises, the neural series includes neurals with an even number of sides. Thus, the seven-sided neurals would probably be eight-sided and the five-sided neural would probably be four-sided in other specimens of *Testudo kaiseni*.

*Testudo lunanensis* Yeh, 1963a:50

*Type*.—IVPP V.1032, damaged plastron with left plastral bridge. Type locality: Wa-ya-chung, Ta-i-ma, Lunan, Yunnan. Horizon: Early Oligocene.

*Remarks*.—Yeh (1963a) distinguished this species, which is the largest tortoise known from China, primarily on the basis of size. He believed it to be closely related to *T. yunnanensis*, the other giant tortoise preserved in Chinese deposits. Auffenberg (1974) referred this species to the synonymy of *T. yunnanensis*. With reservation Auffenberg allocated this latter species to *Geochelone*, on the basis of its large size. Only the inside of the plastron, which possesses no particularly diagnostic features has been prepared; it is a very poorly known form in which size provides the only clue to its affinities. Nevertheless, Chkikvadze (1972) allocated this species to his new genus *Ergilemys*. This species is also represented by appendicular material.

*Testudo nanus* Gilmore, 1931:241

*Type*.—AMNH 6692, complete shell. Type locality: East Mesa, Shara Marun Region, Inner Mongolia. Horizon: ? Ulan Gochu, Lower Oligocene.

*Remarks*.—Gilmore (1931) anticipated the nomenclatorial change adopted by Loveridge and Williams (1957) in noting the mobile posterior plastral lobe in *Testudo graeca*, *T. nanus* and some other *Testudo*. In *T. nanus*, the supracaudal scute is divided, but whether it is divided on both the inside and outside of the pygal bone is not known. In *Geochelone emys* and *G. impressa* it is divided on both sides, but in *T. hermanni* and *Malacochersus tornieri* it is usually divided only on the outside of the shell. Other characteristics of *T. nanus* include an elongated prominent epiplastral projection, gular scutes that do not overlap the entoplastron which is in turn broadly overlapped by the pectoral scutes, two suprapygals with the smaller elliptical ventral element embraced by the larger superior element, and no constriction at the anal border. Gilmore (1931) was not able to locate the anal/femoral sulcus. However, detailed examination of the type material and examination of photos and Gilmore's plates suggests that the anal scute is broader than the femoral; the typical condition for *Testudo*. Only the posterior neural bones are known: ?-?-?-?-4-6-6-6.

Mlynarski (1968) was uncertain about the status of this species but was convinced that it is not referable to *Indotestudo*. Auffenberg (1974) allocated this species to *Geochelone*, subgenus questionably *Indotestudo*. I return this species to *Testudo* because of the mobile plastral lobe and the apparent large size of the anal scute.

*Geochelone oskarkuhni* Mlynarski, 1968:91

*Type*.—Z. Pal. MgCh/15, a plastron and a pygal region from the same individual. Type locality: Altan, Teli, Dzereg Valley, Western Mongolia. Horizon: Pliocene (*vide* Gradzinski *et al.* 1968:75).

*Remarks*.—The allocation of this species to *Geochelone* was accepted with reservation by Auffenberg (1974). Mlynarski (1968) noted similarities between *G. oskarkuhni*, and *Testudo sphaerica* Wiman and *T. kegenica* Khosatsky (1953). He also noted that material of *G. ulanensis* was in too poor a condition to allow meaningful comparisons. In order to express his ideas of phyletic relationships for Asian tortoises, Mlynarski coined the term “hipparionum” group and placed *G. oskarkuhni* within this group. He noted that this species group may be intermediate between *Geochelone* and *Testudo* and perhaps ancestral to the *antiqua-graeca* phyletic line.

The gulars, but not the pectoral scutes, overlap the entoplastron. The cervical scute is long and narrow and there are two suprapygal elements. The larger superior element embraces the more ventral, elliptical element. Mlynarski (1968) admitted that the bad condition of the material makes detailed descriptions largely a product of guesswork.

*Kansuchelys ovalis* Yeh, 1963a:33

*Type*.—IVPP V.1007, nearly complete shell. Type locality: Unknown (? Yushe, Shansi). Horizon: Unknown.

*Remarks*.—Yeh (1963a) distinguished this species from *K. chiayukuanensis* on the basis of plastral scute and bone patterns. He further hypothesized that *Kansuchelys* was more primitive than *Testudo*, but closely related. Auffenberg (1974) suggested that a specimen with such inexact data should not have been described.

The entoplastron is overlapped by the gular scutes but not by the pectoral scutes. The supracaudal scute is entire and the anals are longer medially than the femorals. There are two suprapygals, the larger superior element embracing the inferior elliptical element. The neural pattern is 4-6-6-6-6-6-6, and the hexagonal neurals are short-sided anteriorly.

*Testudo shansiensis* Wiman, 1930:38

*Type*.—IVPP (Catalogue number not published), complete carapace, and plastron missing the anterior lobe. Type locality: southern part of locality 114, Shansi, Ho-Ch'u-Hsien, SE 60 li (1 li equals about one-third of a mile) of Nan-Skha-Wa, 1 li from Ma-Hua-T'an. Horizon: Pliocene.

*Remarks*.—Yeh (1963) referred two IVPP specimens to this species (IVPP V.1015, V.1016) and noted its similarity to *T. hypercostata*. Auffenberg (1974) allocated this form to the synonymy of *T. hypercostata*, which has the same type locality.

The large dorsal suprapygal element is asymmetrical; only one ‘arm’ embraces the smaller elliptical ventral suprapygal. The anal and femoral scutes have similar median lengths. The gulars overlap the entoplastron. The pectoral scutes form a V-shaped sulcus which is posterior to the entoplastron on the midline but overlaps it laterally. This is similar to the condition in *Testudo horsfieldii*. The supracaudal

is entire. The neural formula is 4-8-4-8-4-6-6. Three marginal scutes contact the second pleural scutes. Whether a valid species or not, this form is certainly referable to *Testudo*.

*Testudo sharanensis* Yeh, 1965:53

*Type*.—IVPP V.2868, complete plastron, partial carapace missing some elements of right side, and some fragments. A paratype was designated (IVPP V.2868.1) and consists of a complete plastron and a partial carapace. Type locality: Ula Usu, Inner Mongolian Autonomous Region. Horizon: Late Eocene.

*Remarks*.—Yeh (1965) considered this a very primitive species but discounted any close relationship to *Hadrianus* or *Stylemys* since all the neurals of these two are hexagonal whereas one neural (#2) of *T. sharanensis* is octagonal. He distinguished this species from *Sinohadrianus sichuanensis* on the basis of neural pattern differences. The position of the pleuro-marginal sulcus distinguished *T. sharanensis* from *T. ulanensis* Gilmore (1931), in which it extends along the lateral shell below the costo-peripheral suture.

The gular scutes, but not the pectoral scutes overlap the entoplastron. There is plastral constriction at the lateral borders of the anal and gular scutes. The medial length of the anal exceeds that of the femoral scutes. The supracaudal scute is divided. Although Yeh characterizes the cervical as "small," the cervical scute is large and broad in his fig. 3 (1965). There are notches in the anterior edge of the epiplastra. Yeh believes there are three suprapygial elements. I think it more likely that there is a supernumerary ninth neural yielding the following neural formula: 4-8-4-6-6-6-6-4. If this is the case, there are two suprapygial elements showing the primitive condition with the larger element embracing the more ventral elliptical element. These features suggest that this species is referable to '*Manouria*.'

Auffenberg (1974) did not refer to this species in his checklist. Chkikvadze (1973) contended that *T. sharanensis* possesses intergular scutes; I disagree. Mlynarski (1976) referred this species to the Testudinidae *incerta sedis* and noted posterior plastral similarities shared with *Ergilemys*.

*Testudo shensiensis* Wiman, 1930:28

*Type*.—IVPP (Catalogue number not published), complete shell. Type locality: locality 51, Shensi, Fu-Ku-Hsien, W 110 li Wu-Lan-Kou, SE 1 li Pei-Hou-Kou. Horizon: Pliocene.

*Remarks*.—Yeh (1963a) did not comment on the relationships of these species but refers four IVPP specimens to this taxon (IVPP V.1008, V.1009, V.1010, V.1019). Glaessner (1933) allied this form to the *antiqua-graeca* phyletic line. Auffenberg's (1974) cited Gilmore's (1931) [actually 1934] assignment of AMNH material to this species. Gilmore was critical of Wiman's (1930) work and predicted that further study would reveal that fewer species should be recognized.

The gular, but not pectoral scutes, overlap the entoplastron. The median length of the anal scutes is slightly less than that of the femoral scutes. There is no plastral constriction at the lateral border of either the gular or anal scutes. The cervical scute is relatively large according to Wiman's (1930) figure (Pl. V, Fig. 1). Three marginal scutes (numbers 5, 6 and 7) contact the second costal. The



Fig. 1. Localities in China and Mongolia where testudinid fossils have been unearthed (taken mostly from Yeh 1963a). The shaded area in the lower left is the present distribution of land tortoises in southeast Asia.

neural formula is 4-8-4-6-6-6-6-6. There are two suprapygial elements of about equal size divided by a transverse suture. This species is best allocated to *Tes- tudo*.

*Sinohadrianus sichuanensis* Ping, 1929:232

*Type*.—Geological Survey of China (Catalogue number not published), nearly complete shell. *Type locality*: "It was collected from Fan Chuan of Si Chuan Hsien, Honan Province by Mr. C. Li, . . . . The locality, where the specimen was secured, is near the border of Chieh Chia Chi of Chun Hsien, Hupei Province, where Mr. Li's party happen to go across the boundary line between the two provinces while surveying" (Ping 1929:231). I have tried to locate this ambiguous type-locality without success. It is likely that this specimen was found north of the Han River on the northwestern border of Hupei Province and the southwestern border of Honan Province in the Mot'ien Ling Mountains. *Horizon*: Late Eocene.

*Remarks*.—Auffenberg (1974) suggested that *Sinohadrianus* is more primitive than North American *Hadrianus* and concurs with Yeh (1963a) that it is not



closely related to *Hadrianus* (=junior synonym of *Manouria*, according to Auffenberg 1971).

The entoplastron is not overlapped by the pectoral scutes. Because the epiplastra and the anterior entoplastron are missing, it is not possible to determine if the gular scutes overlap the entoplastron. Other plastral sutures are faint, but it seems that the median length of the anal and femoral scutes are near the same. Both the anterior and posterior margins of the carapace are missing, so it is impossible to determine the morphology of the cervical, suprapygal(s), and supracaudal(s). The neural formula is 4-6-6-6-4-6-6-6, and there may be a ninth neural whose shape is uncertain.

Mlynarski (1976) included this species in the Testudinidae *incerta sedis*. If this species is a tortoise it might be referable to '*Manouria*.'

*Testudo sphaerica* Wiman, 1930:33

*Type*.—IVPP (Catalogue number not published), nearly complete carapace and plastron missing posterior lobe. Type locality: locality 110<sub>2</sub>, Shansi, Pao-Te-Chou, 25 li NE of Chi-Chia-Kou, 5.5 li NE of Wang-Cia-Liang-Kou. Horizon: Pliocene.

*Remarks*.—Mlynarski (1955) removed this form from the *antiqua-graeca* line claiming its affinities lie with *T. horsfieldii*. He later (Mlynarski 1968) changed his mind and allocated this species to the *Geochelone*. Yeh (1963a) referred four IVPP specimens to this taxon (IVPP V.701, V.1011, V.1012, V.1013). Auffenberg (1974) followed Gilmore (1934) in considering *T. yushensis* a synonym. Yeh (1963a) also referred the type of *Terrapene sinica* (IVPP V.701) and material unearthed from the Pliocene sediments of Yushe, Shansi (IVPP V.1011–V.1013) to this species.

The gular, but not the pectoral scutes, overlap the entoplastron. Although the posterior lobe of the plastron is missing in the type, I expect that when discovered the anal scute will have about the same median length as the femoral scutes. There are two suprapygals of uncertain shape. The shape of the cervical scute is unknown. Only the anterior five neurals are known; the neural formula is 4-8-4-8-4?-?-?. Three marginal scutes contact the second pleural scute. Whether valid or not, this form is best allocated to *Testudo*.

*Kansuchelys tsiyuanensis* Yeh, 1979:310

*Type*.—IVPP (Catalogue number has not been published), complete shell. Type locality: Jiyuan, Henan Province. Horizon: Eocene.

*Remarks*.—This recently-named species is very primitive as Yeh (1979) noted. Neither the gular nor the pectoral scutes overlap the entoplastron. There is slight plastral constriction at the lateral anal border, but no constriction at the lateral gular border. The median length of the anal scutes is only slightly less than that of the femoral scutes. There are faint notches in the anterior lip of the epiplastral projection. The pectoral scutes narrow abruptly as they extend medially. The cervical is moderately broad dorsally, and may be even broader ventrally. There are two suprapygals; the larger superior element embraces the smaller ventral elliptical element. The supracaudal scute is divided. Most of the neurals are hexagonal with the short sides anterior; the neural formula is 4-6-6-6-6-6-6-6. The costal bones are alternately wide and narrow, medially and laterally. Marginals

6, 7 and 8 contact the second pleural scute. This species is best allocated to '*Manouria*.'

*Testudo tungia* Yeh, 1963b:224

*Type*.—IVPP V.2768, slightly broken carapace. Type locality: *Gigantopithecus* cave, Liucheng, Kwangsi. Horizon: Early Pleistocene.

*Remarks*.—Auffenberg (1974) believed this material is of a *Cuora* species. The neural formula, 4-6-4-4-4-4-?-?, supports this contention. Furthermore, the small size and characteristically emydid shell silhouette suggest that this species is not a testudinid. The plastron is not known.

*Testudo tunhuanensis* Yeh, 1963a:42

*Type*.—IVPP V.1029a, damaged anterior two-thirds of carapace. IVPP V.1029b, a complete plastron, is a paratype. Type locality: Taben-buluk, Tunhuang, Kansu. Horizon: Unknown (? Miocene).

*Remarks*.—This species was described but not named by Bohlin (1953). Yeh (1963a), followed by Auffenberg (1974), noted the similarity between this form and *T. sphaerica*.

The gular, but not the pectoral scutes, overlap the entoplastron. The median length of the anal scutes exceeds the median length of the femoral scutes. There is no plastral constriction at the lateral gular or anal borders. The cervical is moderate sized. The posterior half of the carapace is unknown. The neural formula is 4-8-4-7-5-6-6-?-?. Probably the odd-sided neurals are in most specimens even-sided, as is usual in tortoises. Marginals 5, 6 and 7 contact the second pleural scute.

*Testudo ulanensis* Gilmore, 1931:245

*Type*.—AMNH 6691, a posterior plastral lobe attached to part of the left bridge, the median part of the plastron posterior of the entoplastron, a costal and peripherals 9, 10 and 11 of both the right and left sides of the carapace with some fragments of costal bones articulated. Type locality: North Mesa, Shara Marun Region, Inner Mongolia. Horizon: Ulan Shireh, Upper Eocene.

*Remarks*.—This difficult-to-allocate species was referred to *Geochelone* by Mlynarski (1968), and retained there with some reservation by Auffenberg (1974). Chkikvadze (1970), without stating his reasons, referred this species to *Hadrianus*.

The median length of the anal scutes is about equal to or exceeds the median length of the femoral scutes. The femoral scutes are separated from the inguinal scutes by the abdominal scutes. This condition is common in *Testudo* and accompanies the development of a hinge in the posterior plastral lobe. There is plastral constriction at the lateral border of the anal scutes, but not at the lateral border of the gular scutes.

*Testudo yunnanensis* Yeh, 1963a:47

*Type*.—IVPP V.1031, portions of anterior plastron. Type locality: Wa-yao-chung, Ta-i-ma, Lunan. Yunnan. Horizon: Early Oligocene.

Table 1.—The recommended nomenclatorial status of Chinese and Mongolian fossil tortoises.

Original trivial name	Original generic name	Recommended generic name
<i>chiayukuanensis</i>	<i>Kansuchelys</i>	'Manouria'
<i>chientutungensis</i>	<i>Testudo</i>	<i>Testudo</i> (?)
<i>demissa</i>	<i>Testudo</i>	<i>Geochelone</i>
<i>hipparionum</i>	<i>Testudo</i>	<i>Testudo</i>
<i>honanensis</i>	<i>Testudo</i>	<i>Testudo</i>
<i>hyercostata</i>	<i>Testudo</i>	<i>Testudo</i>
<i>insolitus</i>	<i>Testudo</i>	<i>Geochelone</i>
<i>kalganensis</i>	<i>Testudo</i>	<i>Geochelone</i>
<i>kaiseni</i>	<i>Testudo</i>	<i>Indotestudo</i>
<i>lunanensis</i>	<i>Testudo</i>	<i>Geochelone</i> (?)
<i>nanus</i>	<i>Testudo</i>	<i>Indotestudo</i>
<i>oskarkuhni</i>	<i>Geochelone</i>	<i>Geochelone</i>
<i>ovalis</i>	<i>Kansuchelys</i>	'Manouria'
<i>shansiensis</i>	<i>Testudo</i>	<i>Testudo</i>
<i>sharanensis</i>	<i>Testudo</i>	'Manouria'
<i>shensiensis</i>	<i>Testudo</i>	<i>Testudo</i>
<i>sphaerica</i>	<i>Testudo</i>	<i>Testudo</i>
<i>sichuanensis</i>	<i>Sinohadrianus</i>	'Manouria'
<i>tsiyuanensis</i>	<i>Kansuchelys</i>	'Manouria'
<i>tungia</i>	<i>Testudo</i>	<i>Cuora</i>
<i>tunhuanensis</i>	<i>Testudo</i>	<i>Testudo</i>
<i>ulanensis</i>	<i>Testudo</i>	<i>Testudo</i> (?)
<i>yunnanensis</i>	<i>Testudo</i>	<i>Geochelone</i>
<i>yushensis</i>	<i>Testudo</i>	'Manouria' (?)

*Remarks.*—Auffenberg (1974) referred this species to *Geochelone* on the basis of size and believed *T. lunanensis* to be a junior synonym. Yeh (1963a) described the form because it is larger than most other Chinese tortoises. Chkikvadze (1972) allocated this species to his genus *Ergilemys*.

The pectorals do not overlap the entoplastron and narrow abruptly as they extend medially. They are slightly broader on the midline than parasagittally. This condition of the pectoral scutes is also present in *Geochelone sulcata* and some *Hesperotestudo* species. The gular scutes overlap the entoplastron. The median length of the femoral scutes greatly exceeds the median length of the anal scutes. There is prominent constriction at the lateral borders of the anal scutes and the postero-lateral tips of the xiphiplastra are elongate and thickened. Most of the carapace is unknown.

*Testudo yushensis* Yeh, 1963a:40

*Type.*—IVPP V.1028, almost complete shell. Type locality: Tsuan-tse-yao, Yushe, Shansi. Horizon: Pliocene.

*Remarks.*—Yeh (1963a) was careful to distinguish this species from *T. honanensis* but did so on the basis of highly variable characters. For this reason, Auffenberg (1974) considered this form a synonym of *T. sphaerica*.

The gular, but not the pectoral scutes, overlap the entoplastron. The median length of the anal scutes is less than the median length of the femoral scutes. Nevertheless, the anal scutes are large and not reduced as in *Geochelone*. There

Table 2.—The stratigraphic position of the testudinids of China and Mongolia is summarized below. Exact stratigraphic information is, at present, not available for most Chinese sediments. Correlation with North American and/or European sediments has not yet been attempted.

Epoch	Species
Pleistocene	<i>tungia</i> *
Pliocene	<i>hipparionum</i> , <i>hypercostata</i> , <i>oskarkuhni</i> , <i>shansiensis</i> , <i>shensiensis</i> , <i>sphaerica</i> , <i>yushensis</i>
Miocene	<i>chienfutungensis</i> (?), <i>honanensis</i> (?), <i>insolita</i> , <i>tunhuanensis</i> (?)
Oligocene—Late	<i>lunanensis</i> , <i>yunnanensis</i>
—Early	<i>demissa</i> , <i>kaiseni</i> , <i>nanus</i> (?)
Eocene—Late	<i>chiayukuanensis</i> (?), <i>sharanensis</i> , <i>sichuanensis</i> , <i>ulanensis</i>
—Middle or Early	<i>tsiyuanensis</i>
Unknown horizon	<i>kalganensis</i> , <i>ovalis</i>

\*—not a testudinid, probably *Cuora* (Auffenberg, 1974).

(?)—stratigraphic position uncertain.

is some plastral constriction at both the gular and anal lateral borders. The cervical scute is large and broadest posteriorly. There are two suprapygal elements; the larger superior element embraces the ventral elliptical element. The supra-caudal is entire. The neural formula is 4-6-4-8-4-6-6-6. This species may best be allocated to '*Manouria*.'

#### Discussion

Although simple classifications have been advanced, there are no comprehensive phylogenetic hypotheses that incorporate Chinese and Mongolian fossil tortoises. Hypotheses have been formulated by allocating species to particular genera; subsequent re-allocation, although reasonable, often did not include discussion of the data upon which the re-allocations rely (Auffenberg 1974). The above checklist constitutes the first step in a re-assessment of the phylogenetic relationships of oriental fossil testudinids. However, this review relies extensively upon the literature and not upon a first hand examination of the material at present stored in the IVPP. For this reason, extensive changes in the classification of Chinese and Mongolian tortoises are deferred.

Four genera have been recognized from eastern Asia: *Testudo*, *Geochelone*, *Kansuchelys* and *Sinohadrianus*. None of these are well diagnosed; characterizations prevail instead of comparative diagnoses. I recommend that four genera continue to be recognized, but different genera than those presently accepted. Diagnoses are below.

*Testudo*: *Testudo* is the only testudinid (except *Pyxis* [Bour 1981] and *Gopherus berlandieri* [J. Howard Hutchison, pers. comm.] that develops an incipient hinge correlated with egg deposition in females) which normally possesses a posterior plastral hinge at the femoral-abdominal sulcus. Not all members of this genus have this hinge (e.g., *Testudo horsfieldii*) and it is sexually dimorphic in some species (Loveridge and Williams 1957). Tortoises of this genus differ further from *Geochelone* in possessing enlarged anal scutes whose median length is equal or exceeds that of the femoral scutes. *Testudo* differs from '*Manouria*' by possessing

an entire supracaudal scute. *Testudo* is distinguished from both of the above genera in having undifferentiated marginals in which three marginals contact the second pleural scute (Roger Bour, pers. comm.). In *Testudo*, unlike *Indotestudo*, the pectoral scutes do not overlap the entoplastron; or if such overlap occurs it is parasagittal rather than medial.

*Geochelone*: *Geochelone* differs from all other Chinese tortoises except *Indotestudo*, by possessing small anal scutes whose median length is very much less than the median length of the femoral scutes. Unlike *Indotestudo*, the pectoral scutes do not overlap the entoplastron.

*Indotestudo*: This genus differs from all other tortoise genera by possessing a transversely extending humeral-pectoral sulcus which crosses the entoplastron. Bour's (1980) elevation of this subgenus of *Geochelone* to generic level is followed.

'*Manouria*': This primitive genus may or may not be monophyletic. It differs from all other tortoises in having a divided suprapygal which is always divided on both its dorsal and ventral surfaces. (In *Malacochersus* and *T. hermanni* the supracaudal is entire ventrally and divided dorsally.) Furthermore, unlike most tortoises, except *Styemys*, the neurals are hexagonal and tetragonal, and usually not octagonal. Recent '*Manouria*' (i.e., *Geochelone emys* and *G. impressa*), sometimes have octagonal neurals anteriorly. Also unlike most other tortoises, except *Malacochersus*, the epiplastral projection is not greatly thickened, but is flattened and often concave upon its dorsal surface. *Hadrianus* is included within '*Manouria*' as suggested by Auffenberg (1971). *Kansuchelys* and *Sinohadrianus* are here referred to '*Manouria*.' '*Manouria*,' although easily recognizable, is presently diagnosed by shared primitive features.

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